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New fossils of *Bos primigenius* (Artiodactyla, Mammalia) from Nihewan and Longhua of Hebei, China

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Abstract The new fossils of *Bos primigenius* in this study came from two regions in Hebei Province: Nihewan Basin (one partial skull with right horn-core and one humerus) and Longhua County (one humerus, one tibia, 2 calcanea and 3 astragali). The humerus from Nihewan has a total length of 457.3 mm, which almost represents the largest aurochs individual which has a two-meter shoulder height. The biggest humerus and other big cranial specimens in northern China can be correlated with the European counterparts of late Middle Pleistocene, and they should be contemporary. The smaller sized limb-bones from Longhua were unearthed from loess deposits, which can be attributed to Late Pleistocene. The current knowledge shows that aurochs may have arrived in China earlier than Late Pleistocene, because its associated taxa, e.g. *Canis lupus*, *Panthera tigris*, *Mammuthus primigenius*, *Equus caballus*, *Coelodonta antiquitatis*, *Sus scrofa*, *Camelus knoblochi*, *Cervus elaphus*, *Alces alces* and *Bison priscus* have appeared as early as late Middle Pleistocene or even earlier in Eastern Europe and Northern Eurasia. Furthermore, new numerical dating results show that the aurochs' occurrences from some sites in China can be traced back to Middle Pleistocene. This study proposes that the larger sized aurochs should be of a late Middle Pleistocene age. In China, aurochs fossils mainly occur in the northern part and the transitional zone along the Huaihe River, but are absent in southern China and Southeast Asia, which resulted in the hypothesis of "Central Asian Corridor" through which aurochs reached China. In recent years, it is proposed that the earliest ancestor of *B. primigenius* is *Pelorovis turkanensis*, and the genus *Bos* appeared in Eurasia at the beginning of the Middle Pleistocene. The present authors think that the African *Pelorovis* species are too different from the *Bos* lineage in morphology; on the contrary, the early *Bos* species from Siwalik in South Asia resembles *B. primigenius* very much. In China, most of the *B. primigenius* fossils were recovered from fluvio-lacustrine deposits, whereas few of them were from loess deposit, which means that the aurochs fossils could be employed as an indicator of warm climate and wet environment.

Key words Nihewan and Longhua, Hebei, China; Middle-Late Pleistocene; *Bos primigenius*; horn-core, limb-bones

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1 Introduction

The genus *Bos* is characterized by a robust postcranial skeleton and a highly derived cranial morphology. It is not difficult to distinguish *Bos* from other allies within the tribe Bovini by the following characteristics: robust skull with elongated and hollowed frontals; there is no preorbital fossa; the premaxilla has a short contact with the nasal bone; the horn-cores are large, posterolaterally inserted and dorsoventrally compressed, with an oval cross-section, going a little backward, outward, forward and slightly upward. *Bos* is a common member of the Eurasian Middle Pleistocene to Holocene faunas, mainly occurred in the Pelearctic Region, but its origin and evolutionary trends are not clear yet. The Asian origin hypothesis (Pilgrim, 1947; Groves, 1981; van Vuure, 2005) and African origin hypothesis (Martínez-Navarro et al., 2007, 2010, 2011, 2014) are still under debates.

Among the extinct species of the genus *Bos*, only aurochs (*B. primigenius*) was recognized in China, and it used to be regarded as an index fossil (Chow, 1953; Pei et al., 1958) or common fossil of Late Pleistocene in North China (Qiu, 2006). But the recent dating result shows that some of the aurochs fossil bearing sites can be traced back to the late part of Middle Pleistocene, such as Dingcun Loc. 100 (Wu and Liu, 2002), Xujiayao (Tu et al., 2015) and Salawusu (=Sjara-osso-gol) (Li et al., 2001), which means the geologic occurrence of *B. primigenius* in China should be reconsidered.

Recently, two specimens of *B. primigenius* were recovered in the Nihewan Basin (Fig. 1), a partial cranium with horn-core resulted from excavation at Heyaozhuang Site and a humerus collected by the local people in Yangyuan County. Although the two specimens were from areas still undergoing debates in strata dividing in Nihewan Basin, the preliminary field

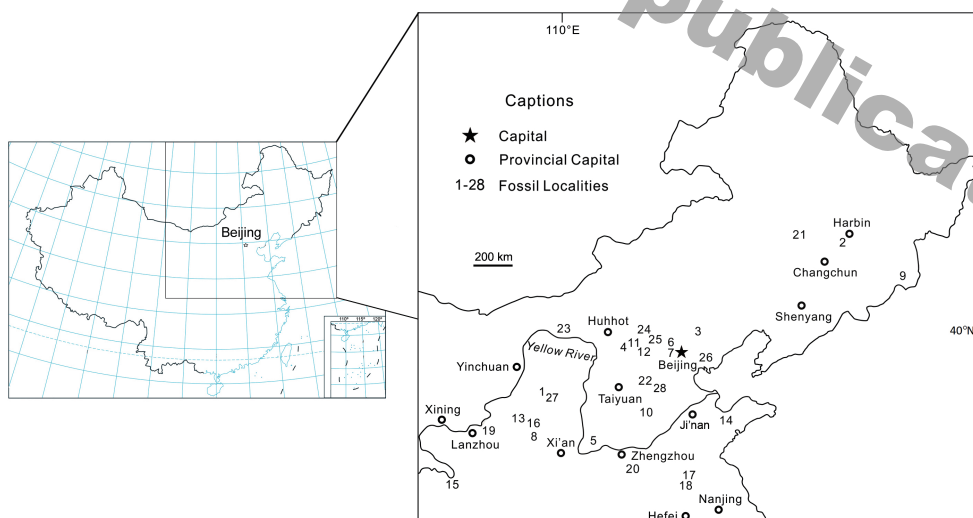


Fig. 1 Sketch map showing the reported fossil localities of *Bos primigenius* in China

1. Salawusu (=Sjara-osso-gol); 2. Guxiangtun (=Kuhsiangtung); 3. Longhua; 4. Datong; 5. Dingcun; 6. Zhuwo;
7. Liulinguan; 8. Qingyang; 9. Wangqing; 10. Xingtai; 11. Xujiayao (=Hsuchiayao)-Houjiayao; 12. Dingjiabu;
13. Loufangzi; 14. Wujiacun; 15. Aba; 16. Rouyuan; 17. Suxian; 18. Mengcheng; 19. Baiyin; 20. Lingjing;
21. Qian'an (Jilin); 22. Shijiazhuang; 23. Baotou; 24. Shangshazui; 25. Heyaozhuang;
26. Qian'an (Hebei); 27. Leilongwan; 28. Zhaoxian

investigation shows that they did not come from the Early Pleistocene Nihewan Beds, instead, they probably came from younger geological settings. The newly recovered specimens are prominently larger than the usual aurochs specimens, and they are crucial for the study of the evolution of the *Bos* lineage in China.

2 Materials and methods

2.1 Fossil materials

New fossils 1) Heyaozhuang Site: right horn-core with partial frontal bone (2013HYZ:42); 2) Shangshazui Site: left humerus (IVPP V 23311); 3) Longhua County: left humerus (V 23312.1), left Mc III+IV (V 23312.2), left tibia (V 23312.3), one right and one left (partial) calcaneum (V 23312.4,7), two right and one left astragalus (V 23312.5,6,8), left malleolus (V 23312.9).

The horn-core was unearthed at Heyaozhuang in 2013 by HPICR; the humerus specimen was recovered at Shangshazui in 2012 by the local people. The Late Pleistocene fossils were unearthed from the loess at a brickyard near the Longhua Town in 2005 by Tong H W and Li Q J.

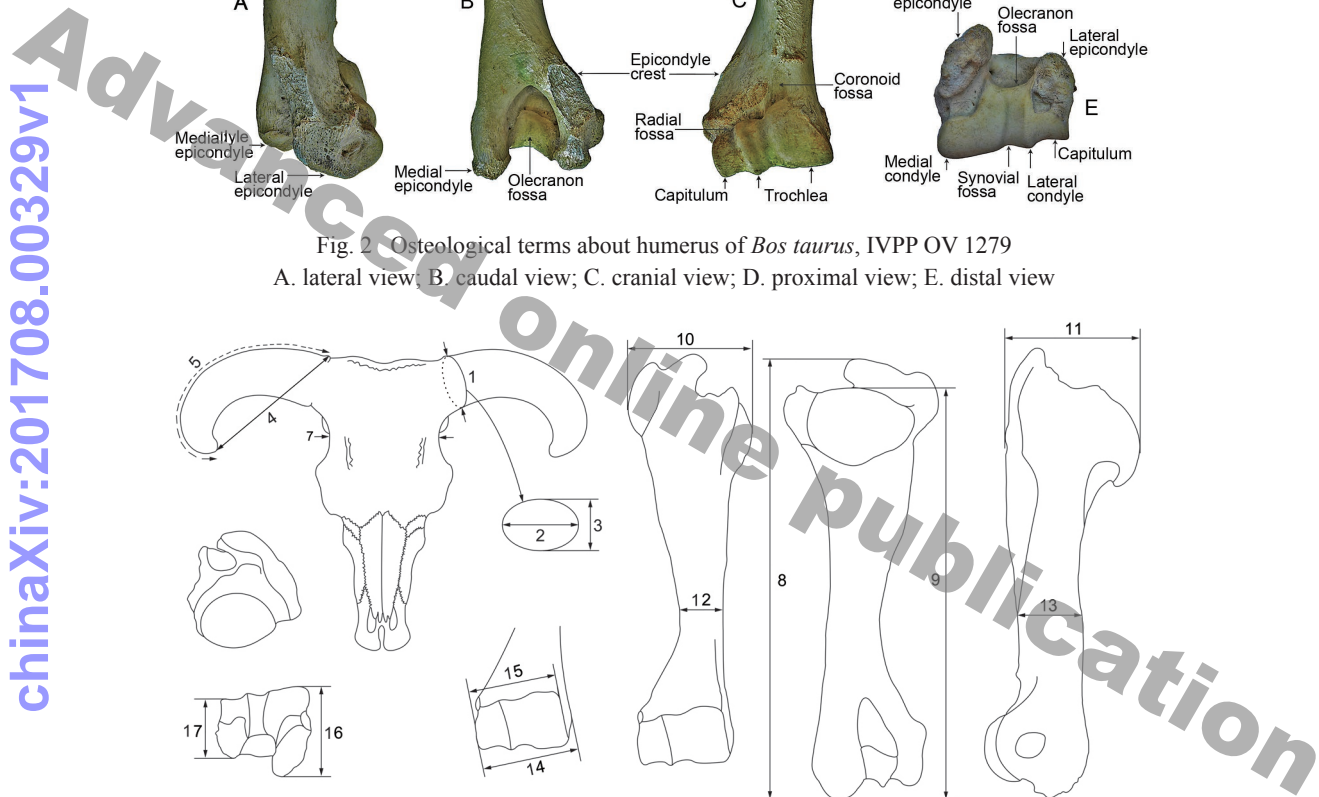
Restudied fossils of *Bos primigenius* from northern China Specimen IVPP V 803 is a partial skull with two horn-cores from Zhuwo of Xishan in Beijing, it was simply described and measured but without image in Hu's report of 1956. Specimen A is a horn-core from Xujiayao-Houjiayao Site, it was only mentioned in the fossil checklist (Chia et al., 1979), but not studied yet. The specimen is exhibited in the Site Museum of Nihewan, but without a catalog number. Specimen B is a partial skull with two broken horn-cores from Holocene deposits at Dingjiabu Reservoir in Nihewan Basin, and it was simply described and measured by Jia and Wei (1980). The specimen is exhibited in the Site Museum of Nihewan, but without a catalog number.

2.2 Terminology and measurements

The osteological terms (Fig. 2) were adopted from Barone (1976), Gentry (1992) and Gee (1993). The post-cranial bones were identified with the method proposed by Sala (1986). The specimens were measured according to the methods used by Gromova (1931) and Martin (1990) (Fig. 3). The measurements were taken with sliding calipers and tapeline in millimeters. The classification system is after Grubb (2005).

Osteological terms are illustrated in Fig. 2. Additional synonyms are listed as follows: Greater tuberosity = Lateral tuberosity; Greater tuberosity (cranial) = summit of greater tuberosity; Greater tuberosity (caudal) = convexity of greater tuberosity; Infraspinal facet = middle facet of greater tuberosity = infraspinal insertion; Lesser tuberosity = medial tuberosity.

Abbreviations Holo, Holocene; HPICR, Hebei Province Institute of Cultural Relics; IVPP, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences; L, Late; M, Middle; OV, Prefix to the catalogue numbers of extant specimens in IVPP; Plei, Pleistocene; T, Fluvial terrace; V, Prefix in catalog numbers for vertebrate fossils in IVPP.



A. lateral view; B. caudal view; C. cranial view; D. proximal view; E. distal view

The image contains several line drawings of sheep bones with numbered measurement points:

- Skull (Top):** A dorsal view of a sheep skull with horns. Numbered points include: 1 (ear hole), 2 (eye socket width), 3 (eye socket height), 4 (horn base angle), 5 (horn tip), 6 (nasal bone), 7 (nasal bone), 8 (nasal bone), 9 (nasal bone), 10 (ear hole to eye socket distance), 11 (ear hole to ear hole distance), 12 (ear hole to ear hole distance), 13 (ear hole to ear hole distance).
- Skull (Bottom Left):** A lateral view of a sheep skull with horns. Numbered points include: 14 (ear hole), 15 (ear hole), 16 (ear hole), 17 (ear hole).
- Leg Bones:** Three line drawings of leg bones (femur, tibia, and radius/ulna) with numbered points 1 through 17 indicating various measurement locations.

3 Systematic paleontology

Class Mammalia Linnaeus, 1758

Order Artiodactyla Owen, 1848

Suborder Ruminantia Scopoli, 1777

Superfamily Bovoidea Gray, 1821

Family Bovidae Gray, 1821**Subfamily Bovinae Gray, 1821****Tribe Bovini Gray, 1821****Genus *Bos* Linnaeus, 1758**

Diagnostic characters (osteological) (emended from Lydekker, 1878; Pilgrim, 1939; 1947; Groves, 1981) Frontal region flat or concave; frontal much elongated; facial part relatively short, and bent down on basicranial axis at an angle of about 20°. The parietal has been shifted into almost the same plane as the occipital which forms an acute angle with the plane of the frontals. The horns have increased considerably in size, and are shifted to the extreme hinder end of the frontal, and are close to the occipital crest; they situated far apart and diverge at an angle of as much as 180°; they usually have an outward and forward curvature at first, after which they bend somewhat upwards and inwards, often slightly twisted anticlock-wise; cross-section either compressed or circular or pear shaped. The lachrymal fossa has vanished, but there is an ethmoidal fissure, and the premaxillae just reach the nasals. The posterior openings of the temporal fossae are narrow and are separated by a considerable interval. The basioccipital is triangular with large tuberosities, of which the posterior pair is much expanded transversely.

***Bos primigenius* Bojanus, 1827**

1898 *Bos taurus primigenius* (Bojanus, 1827), Lydekker, p. 10–14

1953 *Bos primigenius primigenius* (Bojanus, 1827), Chow, p. 187–191

2005 *Bos taurus primigenius* (Bojanus, 1827), Grubb, p. 692–693

2008 *Bos primigenius primigenius* (Bojanus, 1827), Tikhonov, p. 1

For more synonyms see Lydekker, 1898:10–11

Osteological characters (Lydekker, 1878:16–17; 1898:13; Reynolds, 1939:11; van Vuure, 2005:131) The robust and long horn-cores postero-laterally inserted with slight twist and close to the occipital crest: usually have an outward and forward curvature at first, then somewhat upwards and inwards, with an oval cross section, lacking keels. The angle between horn-core and frontal surface occurs mainly between 50° and 60°, which is lesser than in *Bos namadicus*. The horns of bulls are larger, with the curvature more strongly expressed than in cows. The intercornual space is straight rather than arcuated as in *B. namadicus*. The elongated and flattened or concave frontals exceed the facial portion of the skull in length. The temporal fossae do not intrude on to the occiput. Premaxillae contact the nasals posteriorly. The orbits are prominent but not forwardly-directed as in *B. taurus*.

3.2 Descriptions

Partial cranium with horn-cores The cranial fossil has partial frontal and partial parietal bones as well as the whole right horn-core preserved (2013HYZ:42) (Fig. 4A1-A4). The frontal is very flat. The parietal has merged with the occipital bones and completely excluded from the cranial roof.

The horn-cores are laterally, then anteriorly and upwardly extended, the distal part is slightly twisted. The surface of the horn-core is rough. The whole horn-core is very stout (Table S01, S02). The cross-section at the distal part is nearly circular, but at the middle portion, it is dorso-ventrally compressed. The horn-core has no well defined pedicle. In lateral view, the horn-core and the frontal surface form an angle of 64° (Fig. 4A2), which is larger than in the Zhuwo specimen (Fig. 4B2) and Dingjiabu specimen (Fig. 4D2), but smaller than that of the Xujiayao-Houjiayao specimen (Fig. 4C2).

Humerus There are two left humeri, one of which is nearly complete (IVPP V 23311) (Fig. 5A1-A4; Table S03) except for slight breakage, and the other is perfectly preserved (V 23312.1) (Fig. 5B1-B6; Table S03). In general, it is extraordinarily stout and much stronger



Fig. 4 Partial skulls with horn-cores of *Bos primigenius* from Nihewan Basin and Beijing area
A. 2013HYZ:42, partial cranium with right horn-core from Heyaozhuang; B. IVPP V 803, partial cranium with two horn-cores, left one was restored, from Zhuwo near Beijing; C. specimen A, partial cranium with left horn-core from Xujiayao-Houjiayao; D. specimen B, a partial skull with two broken horn-cores from Dingjiabu.

A1, B1 and C1, dorsal views; A2 and C2, medial views; B2 and D2, lateral views;

A3, C3 and D3, occipital views; A4, cross section; D1, parietal view

than that of *Bison palaeosinensis* from the Early Pleistocene Nihewan Beds (Tong et al., 2016). In proximal view, the greater tuberosity is very robust, and it occurs at the anterolateral part of the proximal end; but the lesser tuberosity is less developed. The bicipital groove between the greater and lesser tuberosities is very deep. The head is occurred at the posteromedial aspect of the proximal end; at the anterior border of the articular surface, there is a small notch which connects with the fossa that surrounds the head. The deltoid tuberosity on the lateral side is very developed. The teres major tuberosity on the opposite side of the deltoid tuberosity is faint on V 23312.1 but uncertain on V 23311 because of breakage. On the cranial side of the distal end, the coronoid fossa is shallow. At the lateral one third part of the trochlear surface, there exists a sagittal ridge, to its medial side, is the trochlea (or medial condyle), to its lateral side, is the capitulum (or lateral condyle). The articular surface of the capitulum part forms a small upwardly extended vertical facet. The lowest part of the distal articular surface occurs at the medial side of the sagittal ridge. In posterior view, the greater tuberosity is highly protruded above the level of the head. The medial side of the shaft is almost vertical while the lateral side is concave. The olecranon fossa is very deep and expanded downward, which is narrower and higher than in *Bison* species. The medial and lateral epicondyles are very robust, and they are nearly equally developed; but in *Bison* species, the medial epicondyle extends more downward and stouter than the lateral one. In medial view, the distal extremity of the medial epicondyle stays at the same level as the trochlea does. When viewed laterally, the majority part of the head is hidden behind the greater tuberosity, and there exists a big notch under the head and the head protrudes posteriorly; at the distal end, the lateral epicondyle stops at a higher position than the inferior border of the capitulum. The fossa for muscle attachment on the lateral condyle is smaller and shallow, but in *Bison*, this fossa is usually deep and large as well as roundish.

Mc III+IV The Mc III+IV (V 23312.2) is quite big, with long shaft and expanded extremities (Fig. 6A1-A2; Table S04). In proximal view, there are two large articular facets. The larger facet or magnum trapezoid facet is obviously large, which is articulated with the fused second and third carpals. The smaller facet or unciform facet is triangular and is the articular surface for the fourth carpal. Between the two facets, there exists a narrow groove, the nutrient foramen in the groove is obvious; in *Bison* the same groove is broader. The posterior medial tubercle is moderately developed. In anterior view, the vascular groove (or metacarpal gully) extends below the nutrient foramen near the distal end; the distal extremity looks much more expanded than in *Bison*. In posterior view, a deep groove can be observed between the two proximal facets. The proximal portion of the shaft has a shallow medial longitudinal depression, which does not extend so downward than in *Bison* which results in a more flat posterior surface than in *Bison*. A big nutrient foramen exists near the distal articular surface.

Tibia The tibia has a massive and nearly straight shaft, and with the proximal end much wider than the distal end (Fig. 6B1-B5; Table S05). The vestigial fibula was detached. On the proximal end, the proximal articular surface is composed of two parts: the medial condyle and



Fig. 5 Left humeri of *Bos primigenius* from Shangshazui in Nihewan Basin (A) and Longhua County (B)
 A. IVPP V 23311; B. V 23312.1. A1, B1. cranial views; A2, B2. caudal views; A3, B5. proximal views;
 A4, B6. distal views; B3. lateral view; B4. medial view

the lateral condyle, and the medial one is much larger; the medial side of the intercondylar eminence is slightly higher than the lateral one. On the cranial-lateral side between the tibial tuberosity and the lateral condyle, there exists an indentation or notch called the extensor (or muscular) sulcus. On the cranial side of the proximal end there is a tendon attachment called the tibial tuberosity, below which on the cranial side there is a ridge that runs downward nearly half the shaft called the tibial crest. The sloping surface of the tibial tuberosity is rough. The caudal aspect of the shaft is nearly flat except for some longitudinal muscle scars which are more prominent and have much higher origin positions than in *Bison* species; the posterolateral nutrient foramen is quite pronounced and opens upward; at the lateral edge of the middle shaft, there is a longitudinal groove, which is absent in *Bison* species. On the distal end, the two articular grooves are parallel, while the medial groove is narrower but longer and the lateral groove is much wider, which has a gradually changed lateral boundary rather than a boundary constricting sharply anteriorly as in *Bison* species; between the two grooves, there exists a sagittal ridge, and on the anterior end of the ridge, there is a blunt project which corresponds to the tibial trochlea of the astragalus and is less beak-like as in *Bison* species. At the lateral part, there is a small articular surface articulating with the lateral malleolus (or the distal fibula), which has a shorter antero-posterior but larger transverse dimensions and does not extend to the latero-anterior corner as in *Bison* species.

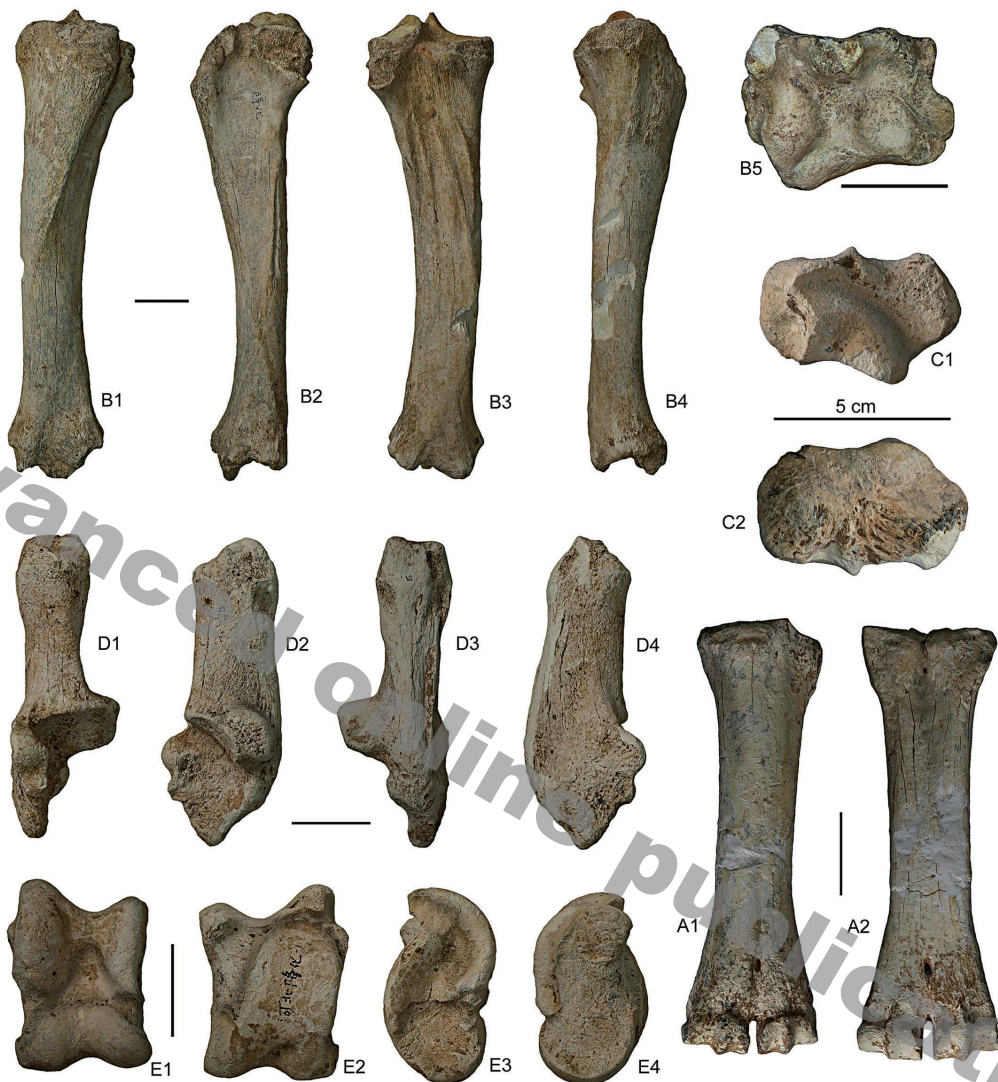


Fig. 6 Limb bones of *Bos primigenius* from Longhua

A. IVPP V 23312.2, left Mc III+IV; B. V 23312.3, left tibia; C. V 23312.9, left lateral malleolus; D. V 23312.4, right calcaneum; E. V 23312.5, right astragalus. A1, B1, D1, E1. cranial views; B2, C2, D4, E3. lateral views; A2, B3, D3, E2. caudal views; B4, C1, D2, E4. medial views; B5. distal view. Scale bars=5 cm

Calcaneum The calcaneal tuberosity (or tuber calcis) is long and robust (Fig. 6D1-D4; Table S06). In distal view, the outline of the distal region is oval-shaped. In anterior view, the tuber calcis is rounded at the tip, but mediolaterally compressed at the shaft; at the upper part of the anterior process there is a trochlear facet, which articulates with the lateral malleolus; the articular surface for astragalus (tibial tarsal) has roundish edges except for the posterior and medial ones; the medial wall of the sustentaculum is nearly vertical rather than inclined as in *Bison*. In medial view, there is no connecting articular surface between the malleolus facet of the anterior process and the astragalus facet; the anterior process is pointed and projects distally

(downward); the situation of the astragalar facet is uncertain because of the poor preservation; the supero-posterior margin of sustentaculum forms a right angle rather than roundish as in *Bison*. In posterior view, the situation of the posterior aspect is unclear because of breakage; the sustentaculum is moderately projected medially and with a straight rather than sloped superior border as in *Bison* species; the naviculo-cuboid facet is narrow and steeply sloped. In lateral view, the distal end is tapered; the proximal part of the lateral malleolus facet protrudes pronouncedly and has a semi-circular outline. In distal view, the naviculo-cuboid (central and fourth tarsals) articular facet is narrow, bended and is also sloped anteroposteriorly.

Astragalus Three astragali (V 23312.5, V 23312.6 and V 23312.8) (Fig. 6E1-E4; Table S07) can be referred to the species *B. primigenius*. In anterior view, there are two proximal trochlear ridges (or condyles), which are parallel to each other and to the sagittal plane, while the lateral ridge is slightly higher; between the two proximal trochlear ridges, there exists a deep saddle-like median groove; the lateral and medial borders of the trochlear condyles are straight. At the distal part, the distal border of the distal articular surface is roundly convex; between the medial and lateral trochlear condyles, there is a broad shallow groove; the medial tubercle is below the line drawn across the proximal margin of the distal trochlea rather than above the line as in *Bison* species. In posterior view, the posterior articular surface for calcaneum is flat but with a subtle sagittal convex, and the superior border of which is tongue-like and its tip reaches the rear surface of the lateral condyle; to the medial side of which there is a wide space, the lateral edge is nearly straight but laterally inclines at the upper part; the medial bottom extends further downwards and is confluent with the distal trochlear surface. The lateral face is trench-like and with anterior and posterior rims and a flat bottom; three facets can be recognized: the one at the posterior rim and at the bottom are for calcaneum and the latter is oval-shaped and covers the distal surface completely rather than like a small rounded pad as in *Bison palaeosinensis*; the one at the anterior rim is for lateral malleolus. It seems that the astragalus of *B. primigenius* has larger breadth/length ratio than the *Bison* species (Table S07).

Lateral malleolus In proximal view, the articular facet for the tibia can be divided into two parts by a sharp conical projection which is less sharp as in *Bison* species. In distal view, the articular facet for calcaneum is concave and broad. In lateral view (Fig. 6C2), the outline is crown-like, and the surface is rugose. In medial view (Fig. 6C1), the facet for astragalus is much broader than in *Bison* species. The greatest depth (anteroposterior dimension) is 56.7 mm.

4 Comparison and discussion

4.1 On classification of Bovini and taxonomic assignment of the studied fossils

The definition of the genus *Bos* confronted serious challenges in the past decades, especially from the molecular evidences. Some scientists expand it through removing the extant species used to be under the genus *Bison* into the genus *Bos* and treated *Bibos*, *Bison*

and *Poëphagus* as subgenera of the genus *Bos* (Groves, 1981); furthermore, some researchers included the extinct genera *Leptobos*, *Epileptobos* and *Pelorovis* into the genus *Bos* (Brugal, 1985; Moyà-Solà, 1987; Hassanin, 2014). Hassanin (2014) intended to combine *Leptobos*, *Epileptobos* and *Pelorovis* into the genus *Bos*, which makes the taxonomic and evolutionary situations of the genus *Bos* more complicated. He also put the origin of *B. primigenius* at ca. 3.5 Ma (Hassanin, 2014: fig. 1.4), but without pointing out its direct ancestor.

On the other hand, some other authors intended to diminish the genus *Bos* through removing some extant species out of it and resurrected the genus *Bibos* (Sokolov, 1953; Hooijer, 1958; Geraads, 1992). It seems that currently the generic name *Bos* is nearly becoming a wastebasket.

Moreover, the traditional classification of the tribe Bovini is clear enough to distinguish the genus *Bos* from *Bison* and *Bubalus* in cranial and horn-core morphological characters, even *Bos* and *Bison* show important differences in the anatomy of the skull and postcranials; meanwhile, their hybridization is possible (Polziehn et al., 1995), which makes the phylogenetic relationship between *Bos* and *Bison* quite confused.

Actually, even in the molecular world, there still exist disagreements about the phylogeny of the tribe Bovini. Based on the mitochondrial cytochrome b gene, *Bos* and *Bison* were grouped together, but they were separated from other Asian and African buffaloes such as *Bubalus* and *Syncerus* (Hassanin and Douzery, 1999). The phylogeny of bovine species based on amplified fragment length polymorphisms (AFPL) (Buntjer et al., 2002) also shows a tree in which *Bison* and yak species (*Bison bison*, *Bison bonasus* and *Poëphagus*) and oxen (*Bos taurus*, *Bos indicus* and *Bos gaurus*) are grouped separately, and are also independent of *Bubalus* and *Syncerus* clade.

At the specific and subspecific levels, the dispute lies at whether “*primigenius*” should be treated as a specific or subspecific name; furthermore, under which species if it is treated as a subspecies. Quite a number of authors treated “*primigenius*” as a subspecies of “*Bos taurus*” (Grubb, 2005), which was proposed as early as 19th century (Lydekker, 1898). Otherwise, “*primigenius*” was used as both specific and subspecific names by other authors (Tikhonov, 2008), and currently the species *B. primigenius* Bojanus, 1827 includes the following subspecies:

Wild †*Bos primigenius primigenius* (Bojanus, 1827), †*Bos primigenius namadicus* (Falconer, 1859) and †*Bos primigenius africanus* (Thomas, 1881) (†: extinct species).

Domestic *Bos primigenius taurus* (Linnaeus, 1758), *Bos primigenius indicus* (Linnaeus, 1758).

According to the morphology and dimensions, all the new fossil specimens in this study can be included in the species *Bos primigenius*, which is much larger than the ancestral species as *B. acutifrons* and *B. namadicus* from South Asia (Table S02).

The horn-core of this study is the stoutest ever recovered in Nihewan Basin, and is more curved than the Xujiayao and Dingjiabu (Holocene) specimens. The basal circumference

and the largest diameter of the horn-core from Xujiayao are 254 and 82 mm respectively. Concerning the humerus, a couple of scholars tried to distinguish the postcranial bones between *Bos* and *Bison* (Gee, 1993), but the result is not so convincing as we expect. The recently discovered fossils are among the largest ones ever referred to the species *B. primigenius*, especially the humerus, which is the largest ever reported in China.

The cranial fossils referred to *B. primigenius* in China are very unique in morphology except those from Aba (Zong, 1984), which has an arcuated intercornual space rather than straight, and the Mc III+IV is stouter and shorter (Table S04), all of which indicates a closer relationship with *Bos mutus*. Studies showed that *B. mutus* has the stoutest metapodials (wide but short) (Kovarovic and Scott, 2014) and largest body size among the extant species of the genus *Bos* (Leslie and Schaller, 2009).

4.2 Geologic age estimation

B. primigenius fossils in China used to be employed as index fossil of Late Pleistocene age (Chow, 1953), but the recent discoveries in Europe and Africa show that this species originated much earlier than previously thought. The oldest record of *B. primigenius* in Eurasia is at Venosa-Notarchirico, Italy (0.5–0.6 Ma) (Martínez-Navarro et al., 2010).

The current knowledge shows that the earliest occurrence of *B. primigenius* in Nihewan Basin is from the Xujiayao human site whose geologic age is around 0.2 Ma (Tu et al., 2015).

The bigger humerus (V 23311) in this study was very probably from the Shangshazui Site (IVPP site No. 72120) whose geologic age is still under serious debate. Furthermore, the chronological relationships among the palaeolithic tools and the fossils of *Palaeoloxodon* as well as *B. primigenius* are also controversial. The earliest report (Wei, 1976) said that the *Palaeoloxodon* fossils coexisted with the palaeolithic tool in the same horizon, and the fossil bearing strata should be of an Early Pleistocene age. Later on, fossil of *B. primigenius* was recovered nearby the *Palaeoloxodon* site, and their horizons can be correlated with each other (Wei, 1980). Therefore, the age of the *Palaeoloxodon* site was revised to Late Pleistocene based on the following fossil assemblage: *Struthio* sp., *Ochotona* sp., *Palaeoloxodon namadicus*, *Equus* sp., *Coelodonta antiquitatis*, *B. primigenius*, which is a typical Late Pleistocene faunal assemblage in northern China; and the geologic setting was explained as a river terrace deposit of Sanggan River (T3) (Jia and Wei, 1980). But recently, the site was revisited, and new paleomagnetic dating work was conducted; new results show that the *Palaeoloxodon* horizon is of an Early Pleistocene age, 1.6–1.7 Ma (Ao et al., 2013; Wei et al., 2015), and it was emphasized that the fossil of *B. primigenius* was not from the same horizon as *Palaeoloxodon* (Wei et al., 2015). Anyway, the current knowledge about the mammalian fossils do not support an Early Pleistocene age, because none of the common members of the Early Pleistocene Nihewan Fauna was recovered at the site, such as *Pachycrocuta licenti*, *Hipparion* (*Proboscoidipparion*), *Coelodonta nihowanensis*, *Elasmotherium*, *Paracamelus*, *Eucladoceros*, *Palaeotragus*, *Spiroceros* and *B. palaeosinensis* etc.

Concerning the stratigraphical record of *Palaeoloxodon* in Eurasia, it is still under serious debate. Lister (2004) proposed that the straight-tusked elephants of the genus *Palaeoloxodon* derived in Africa and entered Eurasia at ca. 0.8 Ma, because the earliest reliable records from Europe, China, and the Middle East are all in the range 0.8–0.6 Ma. The post-Villafranchian elephantid in South Asia was represented by *P. namadicus* Falconer & Cautley, 1846, which was originally described from the Narbada (=Narmada) beds, Central India (Hooijer, 1955). Subsequent chronological studies showed that the geologic range of *P. namadicus* is Middle to Late Pleistocene (Badam and Sankhyan, 2009).

If the *Palaeoloxodon* from Shangshazui did coexist with the fossils of *B. primigenius*, it means that the stratum could not be correlated with the typical Nihewan beds, but is younger instead.

The recently discovered Heyaozhuang Site is similar to the Xujiayao Site in geological settings and archaeological findings, the only difference lies at the former site bears plenty *B. primigenius* fossils, but the latter is dominated by equid fossils. Anyway, they should have the same geologic age because of the large aurochs they shared. It is most probable that the currently studied horn-core and humerus specimens from Nihewan also share the same geologic age as the largest European aurochs, which should be late Middle Pleistocene.

With regard to the postcranial bones of *B. primigenius* from Longhua County, they were from the loess deposit, and definitely have a Late Pleistocene age according to the geologic data (BGMHRP, 1989).

Up to now, the fossil records of *B. primigenius* were mainly recovered in northern China (Fig. 1). According to the current knowledge, the fossils of *B. primigenius* in China were mainly unearthed from such deposits as fluvio-lacustrine and fluvial terrace, most of them are of Late Pleistocene age, except for such controversial sites as Salawusu, Dingcun and Xujiayao. According to the present study, the larger sized *B. primigenius* in northern China should be of a late Middle Pleistocene age as their counterparts indicated in Europe; but the smaller sized *B. primigenius* should be of a Late Pleistocene or early Holocene age. The fossils of *B. primigenius* from northeastern China can be exclusively referred to Late Pleistocene because of their smaller size. It is worth mentioning that the remains of *B. primigenius* from the Holocene riverbed deposits of Dingjiabu Reservoir in Nihewan Basin should had been redeposited from the Late Pleistocene stratum, because its size surpassed all the Holocene specimens.

Concerning the associated taxa with *B. primigenius* in northern China, most of which were once regarded as Late Pleistocene index fossils before (Qiu, 2006); while the current knowledge shows that such kind of fossils as *Ursus spelaeus*, *Canis lupus*, *Panthera tigris*, *Mammuthus primigenius*, *Equus caballus*, *Equus przewalskii* (= *Equus ferus przewalskii*), *Coelodonta antiquitatis*, *Sus scrofa*, *Camelus knoblochi*, *Cervus elaphus*, *Alces alces* and *Bison priscus* have appeared in Europe and northern Eurasia as early as late Middle Pleistocene or even earlier (Markova, 2007; Vislobokova and Tesakov, 2013), which means that the geologic age of the aforementioned taxa in China should be reconsidered.

4.3 On body size

Schultz and Hillerud (1978) proposed that the *Bison* species on the Great Plains in North America underwent a progressive diminution in size during the period from Middle Pleistocene to Late Holocene. But the evolutionary pattern of *Bos* species is far from clear enough, mainly because of the shortage of fossil records. Brugal (1985) noticed that *B. primigenius* has very high intraspecific variations both in body size and in form through time and space. The body size of *Bos* species is subject to such factors as evolutionary stage, ontogeny, sexual dimorphism, geologic age, geographical location and climate etc. The studies by Grigson (1978) verified the markedly sexual dimorphism in Holocene *B. primigenius* from northern Europe.

Although no systematical research work was conducted on the progressive changes in body size through time for *B. primigenius*, quite a lot of attempts were made in the past decades.

The measurements of the skull and horn-core used to be most reliable evidences for estimation of body size for *B. primigenius*, although some debates on the horn-core growth are still ongoing. Guthrie (1966) thought that the higher variation found in horn-cores is due to a number of causes. Perhaps the chief variation component is the ontogenetic factor. Horns and horn-cores have no real definitive size. They continue to grow throughout the life of the animal, adding annual increments at the horn base, each generally smaller than the preceding one. On the contrary, other author thought that little or no growth occurs after the horn-core has reached maturity (McDonald, 1981). Furthermore, other authors thought the male bison acquires a mature horn-core length (but not diameter) at about the time the third molars come into wear. The cores are first long and slender and later increase progressively in diameter with age (Skinner and Kaisen, 1947). The current knowledge is that the horn-core of the cow effectively stops growing in length when the animal reaches maturity, but the external keratinous sheath is produced continually through the animal's life. In that way, the horn becomes effectively larger, even after the bone portion has ceased to grow (Davis et al., 2014; Davis, 2016: personal communication). The present study shows that the stoutness of the horn-core correlates with the skull size, but they do not always positively correlate with those of the cranium; some smaller horn-core may match a relatively large cranium and vice versa (Fig. 7; Table S02), which means that we must be careful when we deduce the body size by horn-cores.

The measurements of humerus, radius and metacarpal were also chosen to estimate the body size of the cattle respectively, but the values resulted from these bones are different; generally speaking, the value calculated from the humeral dimensions turned out to be the closest to the actual size (van Vuure, 2014). Humerus measurements show an overall pattern of reduction in size for *Bos* over time, and the specimens from the late Middle Pleistocene site Ilford are remarkably larger than others (Wright, 2013). Standard measurements were calculated from a population of *B. primigenius* from Ilford, Essex, dated to Marine Isotope Stage 7 (Wright, 2013), which corresponds with the numerical age 0.245–0.19 Ma BP. Furthermore, the humerus from Neumark-Nord, a late Middle Pleistocene site (ca. 0.2–0.125

Ma) in Germany, is 471 mm long, which represents the greatest length for *B. primigenius* (van Vuure, 2005)

The humerus of this study is among the largest ones for *B. primigenius*, which indicates the animal should be quite large; according to the conversion factor created by Matolcsi (1970), the withers height of the aurochs could be as high as 1.89 m (457.3 mm×4.14). The longest humerus for Pleistocene *B. primigenius* is 471 mm, which was from the Neumark-Nord site (0.2 Ma) in Germany (van Vuure, 2005). Therefore, the humerus specimen from Nihewan could have a geologic age of late Middle Pleistocene, around 0.2 Ma. Furthermore, it is reasonable to assume that the larger *B. primigenius* specimens in China are also predated the smaller specimens.

The biometrical analysis of the metapodial bones of aurochs from Avetrana shows a trend which is characterized by an increase in size from Middle Pleistocene to early Late Pleistocene and to a decrease in size during the late Late Pleistocene and Holocene, which can be divided into 5 stages in chronological sequence (Pandolfi et al., 2011). A number of previous studies noticed a size decrease in the aurochs between the Pleistocene and Holocene in Europe, but the most prominent size decrease may occur sometime around the last interglacial. This fits well with previous work by Cerilli and Petronio (1991) who concluded by looking just at metapodials, that the aurochs initially increased in size until it reached its maximum dimensions in the Riss Ice Age (ca. 0.13 Ma BP). Nevertheless, body size may have increased again during some of the subsequent cold periods (ca. 85–60 kyr BP) (Wright, 2013).

In addition, the body size changes between regions were also noticed; the southern European aurochs was somewhat smaller than the northern ones, and the west European aurochs were smaller than east European ones (van Vuure, 2014). Some authors also compared the body sizes between the wild aurochs (*B. primigenius*) and the domestic cattle (*B. taurus*), the result shows a tendency of diminution (Guintard, 1999). But the present studies show that the extant species of *Bos* has broad intraspecific variation in body size.

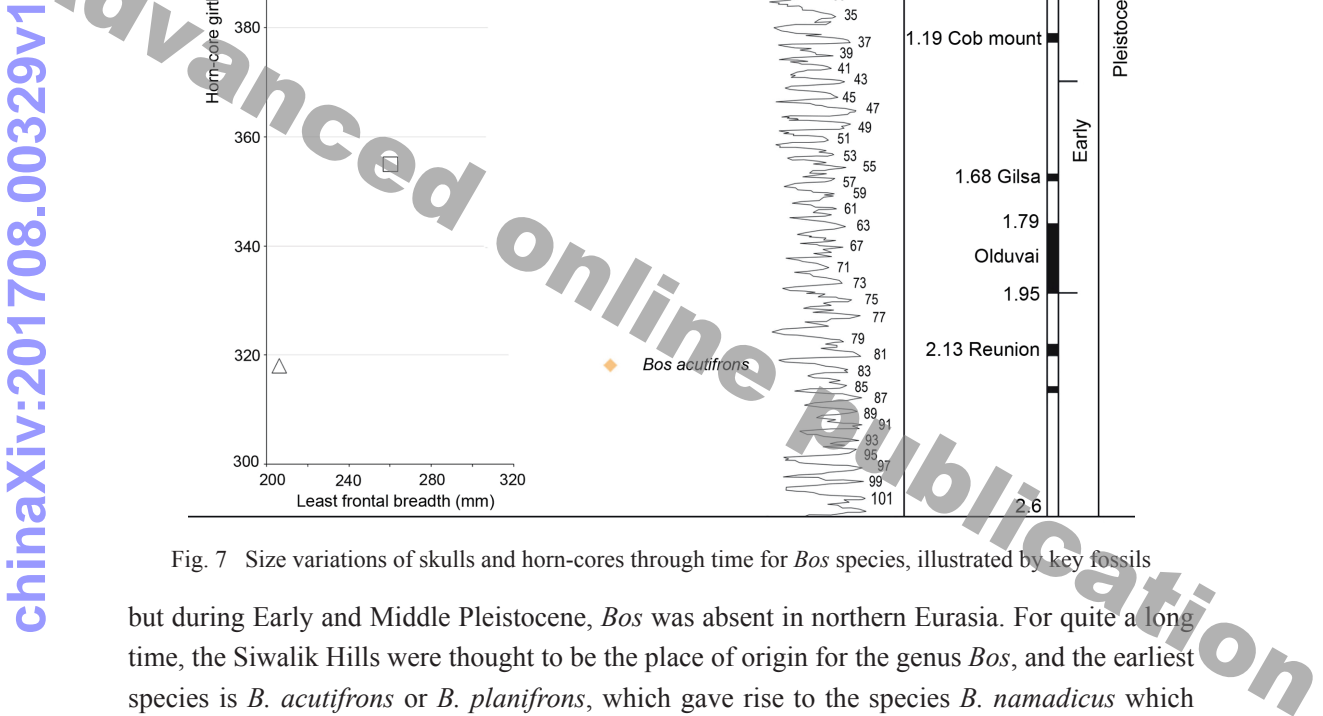
It is worth noticing that *B. primigenius* became common during the late Middle Pleistocene (early Aurelian LMA, ca. 0.35 Ma) in Europe, when the largest *B. primigenius* specimens are recorded (Masini et al., 2013). Therefore, it is reasonable to assume that the big humerus from Nihewan also should indicate an age of late Middle Pleistocene.

4.4 On the origin and evolution of *Bos*

Although the origin place of *Bos* remains unclear, two assumptions have been proposed: South Asian origin and African origin.

For the early fossil *Bos* from South Asia, four species were established successively, namely *B. namadicus* Falconer, 1837; *B. planifrons* Lydekker, 1878; *B. acutifrons* Lydekker, 1878; *B. platyrhinus* Lydekker, 1878. Later on, *B. planifrons* was regarded as the female of *B. acutifrons* by Lydekker, 1897. Currently only *B. namadicus* and *B. acutifrons* are taken as valid names.

The current knowledge shows that the definite early *Bos* only occurred in South Asia,



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Fig. 7 Size variations of skulls and horn-cores through time for *Bos* species, illustrated by key fossils

but during Early and Middle Pleistocene, *Bos* was absent in northern Eurasia. For quite a long time, the Siwalik Hills were thought to be the place of origin for the genus *Bos*, and the earliest species is *B. acutifrons* or *B. planifrons*, which gave rise to the species *B. namadicus* which

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of the genus *Bos* is *B. acutifrons*, which first appeared at the beginning of Pleistocene, i.e. 2.58 Ma and survived to 1.0 Ma BP (Patnaik, 2013). *B. namadicus*, a close relation of the aurochs, is known from fossil remains found in the Middle Pleistocene alluvial deposits of various rivers of peninsular India (Pilgrim, 1947). Therefore, Siwalik Hills were regarded as the center of origin for the genus *Bos* (Colbert, 1935).

Duvernois (1990) proposed that a form of *Leptobos* (*Leptobos*) or *Leptobos falconeri* from the Siwaliks (Pilgrim, 1939), which is in connection with *L. (Leptobos)*, is the ancestor of the Pleistocene genera *Bison*, *Bos* and *Bibos*.

Therefore, the area of origin of the aurochs was most probably in India (Thenius, 1980). The aurochs is estimated to have evolved there between 1.5 and 2 million years ago. In the course of the Pleistocene it spread to other parts of Asia, to northern Africa and to Europe (Koenigswald, 1999).

In recent years, a new scenario of phylogeny for the *Bos* lineage was proposed, which was based on anatomical and morphometric studies, and considered that the evolution of *Bos* lineage took place separately in Africa, rather than in Eurasia as for the lineage *Leptobos*–*Bison*. The genus *Bos* evolved in Africa and dispersed into Eurasia at the beginning of the Middle Pleistocene (Martínez-Navarro et al., 2007). The ancestor of *Bos* is the Olduvai buffalo *Pelorovis oldowayensis* (Reck, 1928) (the species is moved to the genus *Bos* by Martínez-Navarro et al., 2010, 2014), which gave rise to the species *B. buiaensis* at eastern Africa at 1.0 Ma BP, and finally *B. buiaensis* evolved into *B. primigenius* in North Africa (Martínez-Navarro et al., 2010, 2014).

As a result, Martínez-Navarro et al. (2010, 2014) proposed that *B. buiaensis* was the oldest modern large form of the genus *Bos* and distinguished the following species in the genus: 1) *B. turkanensis* for the Early Pleistocene African forms, with a cranium which is proportionately more elongated and a primitive dentition that shows a marked spur in the distal face of the metaconule of the upper molars; 2) *B. oldowayensis* for the late Early Pleistocene forms of Africa and the Levantine Corridor, younger than the Olduvai normal subchron and older than the Jaramillo normal subchron, which is usually larger and has a cranium more robust than *B. turkanensis*; 3) *B. buiaensis* for the latest Early Pleistocene forms of Africa and the Middle East; and 4) *B. primigenius* for the Middle Pleistocene–Holocene forms from Africa and Eurasia. At the end of the early Middle Pleistocene, the genus *Bos* spread from Africa, being first recorded in Europe at Venosa-Notarchirico (0.5–0.6 Ma) (Martínez-Navarro et al., 2007). *B. primigenius* has been recorded in the early Middle Pleistocene only in southern and central Europe, reaching northern Europe in MIS 11, the oldest records for Britain being at Clacton (Essex) and Swanscombe (Kent) (Stuart, 1982; Breda et al., 2010). The earliest remains of the aurochs in Germany date from about 0.275 Ma ago (van Vuure, 2005).

The present authors think that the species group of *Bos* from South Asia is much closer to *B. primigenius* in cranial morphology and horn orientation (Fig. 8), and the *Pelorovis*–*Bos* hypothesis is not supported by the following evidences: 1) the angle of horn divergence in

Pelorovis is not coincide with that of *Bos* species; 2) in *Pelorovis* there is almost no postorbital constriction; 3) the orbits are too near to the horn-cores and are not projected outwardly; 4) between the early species of *Bos* from Siwalik and the *Pelorovis* species, the former resembles *B. primigenius* more strongly; 5) the metacarpals of *Pelorovis* are too short and too robust (Gentry, 1967) for *Bos* species.

Furthermore, Bar-Yosef and Belmaker (2016) proposed that *B. primigenius* appeared in southwestern Asia as early as 1.2 Ma BP, and it continually occurred in this region until Late Pleistocene. The *Pelorovis*–*Bos* hypothesis cannot explain the appearance of *B. primigenius* at such an early time in southwestern Asia.

Except the Siwalik area, the fossil records of early *Bos* spp. in other parts are scanty. Maybe the Early Pleistocene fossils of *Bos* (*Poëphagus*) spp. from Central Asia can provide some extra allusions for the evolution of the bovine lineage; at least they look much similar to *B. primigenius* than the African *P. oldowayensis* does.

4.5 *Bos primigenius* and paleoenvironment

During the Pleistocene, the cold and warm periods alternated. Although the early works showed that *B. primigenius* occurred in both glacial and interglacial stages (Kurtén, 1968), the recent studies indicated that *B. primigenius* was an interglacial animal (Kolfshoten, 2000; Koenigswald, 2007). It seems that the latter proposal got support from the fossil records, which shows that the fossils of *B. primigenius* and *Bison* spp. seldom coexisted at the same site or/and the same layer in the western European faunas (Brugal, 1985: table 1). *Bison* fossils

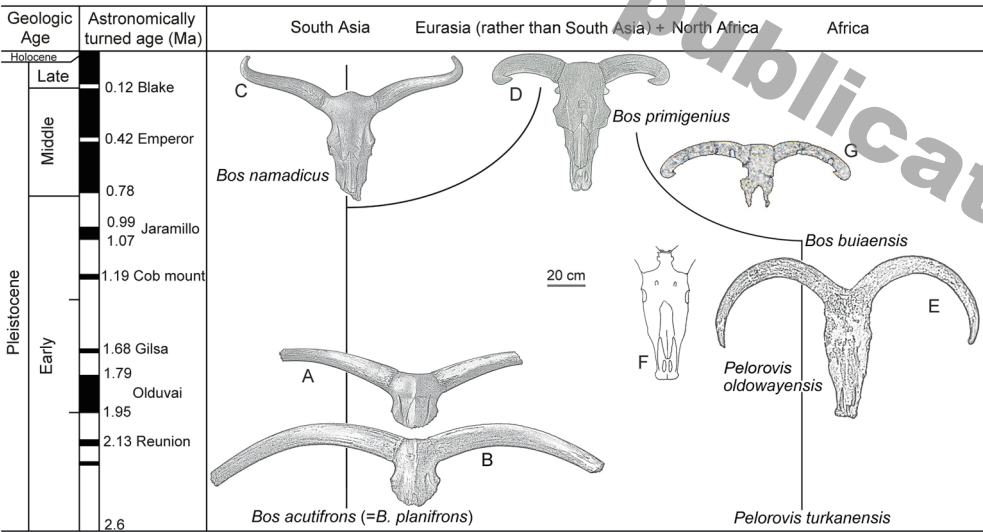


Fig. 8 Evolution of *Bos* lineage: explained by two hypotheses and key fossils
Left column, the South Asian origin scenario; right column, *Pelorovis*–*Bos* lineage. The photos of *Bos acutifrons* (A and B) from Siwalik and *B. namadicus* (C) from Narmada were modified from Lydekker (1878); the photo of *B. primigenius* (D) from Ilford was modified from Stuart (1982); the photo of *Pelorovis oldowayensis* (E) was modified from Leaky (1965); the line drawing of *P. oldowayensis* (F) was adopted from Gentry (1967); the photo of *B. primigenius* from Wadi Sarrat (G) was modified from Martínez-Navarro et al. (2014)

are usually associated with cold-adapted faunas. In Europe, the aurochs withdrew during cold periods to the Mediterranean area and expanded in warmer periods to the north (Koenigswald, 1999). Obviously they were not as well adapted to cold and dry circumstances as were woolly mammoths (*Mammuthus primigenius*) and woolly rhinos (*Coelodonta antiquitatis*), steppe bison (*Bison priscus*) and horses (*Equus*) (van Vuure, 2002).

Bos primigenius is a common member of the Eurasian Middle Pleistocene–Holocene LFAs (local faunal assemblages), particularly abundant in the Italian peninsula during interglacial phases (Martinez-Navarro et al., 2007). The distribution area of *B. primigenius* during Pleistocene stretched across nearly all of Europe and large parts of Asia and North Africa. But it was adjusted by the glacial/interglacial alternations, diminishing in cold periods and enlarging in warmer ones (van Vuure, 2005).

In Europe, aurochs had a special relation with marshes and marshy forests (van Vuure, 2002). In northern China, almost all of the *B. primigenius* fossils were recovered from fluvio-lacustrine deposits, whereas few of them were from loess deposit, which means that the aurochs fossils could be employed as indicator of warm climate and marshy forest environment in general. Nevertheless, the situation in northeastern China is quite complicated, because such kinds of interglacial elements as *B. primigenius* and *Bubalus* spp. were usually mixed with the *Mammuthus*–*Coelodonta* faunas during the Late Pleistocene, whether they occurred alternatively or concurrently is still not clear.

5 Conclusion

The new fossils of *Bos primigenius* in this study came from two regions in Hebei Province: the horn-core and the larger humerus are from Nihewan Basin; the smaller humerus and other limb-bones are from Longhua County. According to the morphological and osteometrical characters, the fossils from Nihewan Basin can be estimated to have a late Middle Pleistocene age; the smaller sized limb-bones from Longhua were unearthed from loess deposit, which can be attributed to Late Pleistocene. *B. primigenius* arrived in China at its evolutionary peak period, i.e. the late Middle Pleistocene, which is earlier than previously thought. In China the larger sized fossils of *B. primigenius* from the following sites should have a late Middle Pleistocene age, such as Zhuwo in Beijing; Shangshazui, Heyaozhuang and Xujiayao-Houjiayao in Nihewan; Dingcun in Shanxi. The smaller sized *B. primigenius*, especially those from northeast China, can be attributed to Late Pleistocene.

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河北泥河湾及隆化新发现原始牛化石

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摘要: 原始牛(*Bos primigenius*)化石新材料包括泥河湾盆地禾尧庄的1件角心、上沙嘴的1件肱骨和承德隆化的1件肱骨、1件胫骨、1件踝骨、2件跟骨和3件距骨; 其中上沙嘴的肱骨化石长达457.3 mm, 代表迄今在我国境内发现的最大原始牛个体, 也是该种的最大记录之一; 推算其所属动物的肩高接近2 m; 北京门头沟珠窝的原始牛头骨的眶后宽度及角心周长数据也是该种的最大记录之一; 禾尧庄的角心标本稍小, 但也比晚更新世多数同类要大; 这些巨大的化石与欧洲中更新世晚期同类十分接近, 其时代也应当与之相当, 为中更新世晚期; 过去认为原始牛在我国只出现于晚更新世地层, 但现在看来该种在中更新世晚期就已扩散到中国。东欧及北亚的最新化石证据表明, 过去认为与原始牛共生的晚更新世化石组合的常见属种早在中更新世晚期或更早时期就已出现, 其中包括灰狼、虎、真猛犸象、马、真披毛犀、野猪、诺氏驼、赤鹿、驼鹿及草原野牛等。最新测年数据也表明中国北方有几个含原始牛化石的遗址是形成于中更新世晚期; 本文认为华北和西北地区个体巨大的原始牛, 代表中更新世晚期, 而个体较小的则可能代表晚更新世或全新世; 近些年在东北地区发现大量原始牛化石, 但其中少见个体巨大者。在我国, 原始牛化石分布只局限于北方及淮河过渡区, 而在南方及毗邻的东南亚地区均未发现此类化石; 因此, 有人提出原始牛很可能是在中更新世中、晚期通过中亚走廊(Central Asian Corridor)进入中国。不过, 近些年在非洲也发现了一些牛属(*Bos*)化石, 因此有人又提出了牛属非洲起源的“奥杜威牛-牛属演化谱系”(Pelorovis-Bos lineage), 但该学说所依据的奥杜威牛化石材料, 在形态结构上与牛属相去甚远, 难以归入同类; 此外, 非洲可靠的牛属化石记录均未超过1 Ma。本文作者支持传统的牛属“南亚起源学说”, 因为在南亚西瓦里克地区发现的早期牛属化石不仅时代更古老(早于2 Ma), 并且在形态上与原始牛更为相似。中国北方的原始牛化石主要发现于华北平原、黄土高原和松嫩平原的河湖相堆积层, 仅极个别出现于黄土地层; 由此推断原始牛可能更喜欢水系发育的林缘和/或沼泽环境。

关键词: 河北隆化, 泥河湾, 中-晚更新世, 原始牛, 角心, 肢骨

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